GROWTH AND REPRODUCTION IN AN ALPINE CUSHION PLANT: *ASTRAGALUS KENTROPHYTA* VAR. *IMPLEXUS*

Wayne R. Owen[1]

ABSTRACT.—A two-year field experiment was conducted to investigate factors hypothesized to affect the reproductive potential of *Astragalus kentrophyta* var. *implexus* and to test the importance of trade-offs between growth and reproduction in this species. Levels of mineral nutrients, water, herbivory, and competition were manipulated. Seed output and growth of individuals in treatment groups were compared against control plants. Neither water nor mineral nutrients alone were shown to affect growth or reproduction. Herbivory was shown to be similarly unimportant in affecting growth and reproduction. Competition with other species influenced growth but not reproduction. No significant trade-offs between growth and reproduction were detected within years. However, there did appear to be a trade-off between these major fitness components when compared between years.

Key words: *Astragalus, alpine, competition, fecundity, trade-off, White Mountains.*

The impact of resource availability on the reproductive output of plants is well established (Harper 1977, Schoener 1983, Fowler 1986, Welden and Slausen 1986). Plants may experience resource limitation as a result of competition (inter- or intraspecific) or poor habitat quality. Resource limitations can also occur when a portion of a plant's photosynthetic organs are removed (e.g., by herbivory), damage which clearly interferes with the plant's ability to provision its offspring (Marquis 1991). A number of authors (Cody 1966, MacArthur and Wilson 1967, Harper 1977, Grime 1979, Tilman 1982, Weiner 1988, 1990) have considered the ecological consequences of resource limitation for individuals and populations and have described various strategies that plants might be expected to pursue to optimize the allocation of limited resources.

This study tests whether the availability of resources limits the fecundity of *Astragalus kentrophyta* Gray var. *implexus* (Canby) Barneby (hereafter, simply *A. kentrophyta*) and to what extent trade-offs between growth and reproduction might influence patterns of reproduction observed in this species. *A. kentrophyta* is an alpine cushion plant indigenous to high elevations throughout the Intermountain West of North America (Barneby 1964).

Many lines of evidence suggest that reproduction in *A. kentrophyta* might be resource limited. Experiments involving other organisms from this habitat have shown that availability of resources influences the competitive ability and distribution of species (Wright and Mooney 1965, Mooney 1966, Marchand 1973), though this is not generally true of all alpine habitats (Korner 1989). Second, standing biomass and percent cover are substantially lower on dolomitic soils than on adjacent sandstone- and granite-derived substrates, suggesting that plants on the dolomite barrens might be relatively resource limited (Mooney 1966, Owen 1991). Third, *A. kentrophyta* plants routinely abort the majority of flowers they produce each year (Owen 1991), a pattern that has been attributed to resource limitations in a broad spectrum of species (Lovett Doust and Lovett Doust 1988).

An experiment was designed (1) to test whether there are resource constraints on the reproduction and growth of *A. kentrophyta* and (2) to assess the interactions between two major components of fitness (i.e., growth and reproduction) under different regimes of resource availability. To do this, a factorial field experiment was established in which separate groups of plants would receive either (1) water or (2) nutrient supplements, (3) protection from herbivory, or (4) relief from the potentially competitive influence of neighbors.

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[1]University of California, Davis, and White Mountain Research Station, University of California, Los Angeles. Present address: Boise National Forest, 1750 Front Street, Boise, ID 83702.

STUDY AREA

The study was conducted on the alpine dolomite barrens of Sheep Mountain Pass above the Patriarch Grove bristlecone pine forest, in the White Mountains of Mono County, CA. Elevations at the site range from 3535 m (11,600 ft) to 3660 m (12,000 ft), and topographic relief of the site is minimal. In the White Mountains *A. kentrophyta* occurs only on dolomitic soils (Lloyd and Mitchell 1973, Hall 1991).

Weather data were obtained from the White Mountain Research Station, Mt. Barcroft Laboratory, located 6 km north of the study site at an elevation of 3800 m. Soils on the dolomite barrens have a high cation exchange capacity and are depauperate in nitrogen, phosphorus, and potassium (Mooney et al. 1962, Wright and Mooney 1965, Brayton and Mooney 1966, Mooney 1966, Marchand 1973, 1974). The moisture-holding capacity of dolomite-derived soils is equivalent to that of adjacent granitic soils (Mooney et al. 1962, Wright and Mooney 1965, Marchand 1973). Vegetation of the White Mountains is generally xerophytic; this trend is especially prevalent on the dolomite barrens (Lloyd and Mitchell 1973).

MATERIALS AND METHODS

In June 1989, 195 healthy *A. kentrophyta* plants were selected randomly from within an area of approximately 0.2 ha. Decadent (senescent) plants were disqualified from inclusion in this experiment. The specific location of the site was chosen for its apparent homogeneity with respect to soil physical characteristics, vegetation, and topographic profile. Plants were randomly allocated to five treatment regimes: (1) 50 plants were provided with three separate 1-L applications of water during the 1989 growing season. Plants were watered during the driest part of the summer (4 July, 2 August, and 19 August) to maximize the beneficial impact of the treatment. Water was applied slowly (to maximize infiltration) in a radius of 12.5 cm around each plant. This treatment supplied 6.1 cm of moisture to each plant. Expected precipitation for the three-month growing season is 8.7 cm (Pace et al. 1968). The 1989 summer precipitation was 1.1 cm. This treatment group will be referred to as "Water." (2) Another 50 plants received supplemental nutrients. These plants were given approximately 17 g of a balanced general-purpose fertilizer (Scott's All-Purpose Builder, 12:10:12 N:P:K), providing each plant with 2.0 g N (in the form of ammoniacal nitrogen, ureas, and water soluble nitrogen), 1.7 g P (from phosphoric acid, P_2O_5), and 2.0 g K (from soluble potash, K_2O). These quantities are equivalent to application rates of 13.8, 11.7, and 13.8 kg ha^{-1}, respectively. A balanced fertilizer was chosen because experiments by Chambers et al. (1987) and Shaver and Chapin (1980) have shown that plants in cold environments respond most vigorously to resource augmentation with fertilizer containing a balance of essential nutrients. The dry fertilizer was scattered in an approximately 2-cm-wide ring around the perimeter of each test plant. Summer seasonal precipitation in 1989 was apparently sufficient to solubilize the fertilizer and deliver it to the soil profile, as the granules had completely disappeared from the surface in approximately one month. This treatment group will be referred to as "Fertilized." (3) A third treatment was designed to protect plants from herbivory and predation on flowers and young fruits. Two locally common insects habitually consume the reproductive parts of *A. kentrophyta*. The more common of these insects, a darkling beetle (Tenebrionidae: Coleoptera), consumes flowers. Larvae of a locally common Lycinid butterfly species (Lycaenidae: Lepidoptera) occasionally consume immature *A. kentrophyta* fruits. "Tangle-foot" brand sticky-trap was applied in a circle around each of 25 plants to exclude potential herbivores. Tanglefoot barriers were repaired as needed. This treatment group will be called "No Predation." (4) The fourth treatment sought to relieve a group of 20 *A. kentrophyta* plants from neighborhood competition. A 0.25-m-radius circle around a central target *A. kentrophyta* plant was cleared of all other plants by cutting them off at ground level. This method minimized ground surface disturbance. Clearings were 0.2 m^2 in area. The average number of neighbors (ramets) removed was 63 (mostly tillers of *Poa rupicola*), covering an average of 15% of the ground surface. Excavations of *A. kentrophyta* plants show that its roots grow straight downward into the soil with minimal lateral root spread (Owen 1991). Roots of the target plants were therefore

thought to be well isolated from interactions with actively assimilating roots of other plants. Plants clipped in the cleared areas were trimmed if they resprouted. Plants in this treatment group are referred to as the "Target" group. (5) A final group of 50 unmanipulated plants was marked as a "Control" group. Size of the experimental groups was based on an analysis of expected variances in responses to the treatments; lower expected variances require smaller necessary samples (Sokal and Rohlf 1981).

Plant sizes (cushion area) were measured and recorded on 23 June 1989, shortly after initiation of growth for the season. Treatments were initially applied on 4 July 1989. In September 1989 all plants were remeasured, and the entire fruit and seed crop produced by each of the 195 plants was harvested. Since *A. kentrophyta* forms a tight cushion that never exceeds 1 cm in height and seeds are not released from the plant before the end of the growing season, there was great confidence that the entire seed crop of each individual was retrieved. In early June 1990 I again measured the area of all plants just as they were initiating growth for the season. Fertilized and Water treatments were not repeated in 1990 so as to evaluate the potential for lags in the effectiveness of resource supplementation. Tanglefoot barriers were maintained during 1990 to test for interannual variation in the effects of herbivores and predators. Clear zones around Target plants were maintained in 1990. All plants were allowed to grow through the season, and in September 1990 all 195 plants were remeasured and all fruits and seeds harvested. No attempt was made to quantify flower production, but previous experience (Owen 1991) had shown that seed production is a significant function of flower production (Owen 1991). Flowers, when aborted, are dropped at a very early age (Owen 1991) and probably represent a minimal per-unit cost in resources to the plant (Bookman 1983, Stephenson 1984). Therefore, the cost of flowers should be proportional to a plant's seed output and can safely be disregarded for the purpose of this work. Fruits and seeds were cleaned and separated in the laboratory, counted, and weighed.

Results

Weight of individual reproductive structures (seeds and fruits) was independent of total numbers of those items produced per plant in both years (Table 1). Average seed and fruit weights were significantly correlated ($R = .429$ in 1989, $R = .443$ in 1990). There were no significant differences between treatment groups for the weight of individual seeds or fruits (results not presented). Because seed production is well correlated with other possible measures of fitness in *A. kentrophyta* and weights of those seeds are independent of the numbers of reproductive structures produced on a plant (Table 1), seed output was used as an index of total reproductive effort.

In a comparison of slopes of regression analyses, growth was a significant function of plant size in both 1989 and 1990 (Table 2), though the relationship was weaker in 1990. The weight of individual seeds and fruits was independent of seasonal growth (Table 2). The amount of growth across years was significantly but poorly correlated.

TABLE 1. Correlation matrix for selected demographic traits. Values above the diagonal are correlation coefficients (R) based on 1990 data; those below the diagonal are derived from 1989 data.

	Seeds produced	Seed weight (average)	Seed weight (total)	Fruits produced	Fruit weight (average)	Fruit weight (total)	Reproductive weight (total)
Seeds produced**	1	.003	.976*	.964*	.143*	.920*	.966*
Seed weight (average)	.042	1	.139*	−.001	.433*	.081*	.115*
Seed weight (total)	.977*	.200*	1	.945*	.229*	.937*	.987*
Fruits produced**	.963*	.024	.033*	1	.106	.963*	.968*
Fruit weight (average)	.136*	.429*	.215*	.074	1	.289*	.260*
Fruit weight (total)**	.943*	.120*	.949*	.952*	.284*	1	.981*
Total reproductive weight**	.973*	.1656*	.989*	.954*	.249*	.985*	1

*Kendall Rank Correlation is significant at P < .05.
**Treatment differences noted with one-way ANOVA. These differences do not affect the magnitude of significance of the correlations.

TABLE 2. Slopes of regressions for selected demographic traits on growth in 1989 and 1990 using the total data set (i.e., not partitioned by treatment). Where the overall regressions are not significant, there were also no treatment differences.

	Growth in 1989	Growth in 1990
Growth in 1990	.168*	—
Plant size	.340*	.110*
Seed weight	−.038	−.054
Fruit weight	.035	.036

*Regressions are significantly positive (P < .05). One-way ANOVAs suggest differences between treatment groups for values of these traits (P < .05).

TABLE 3. Result of an ANCOVA on seed production and growth by treatment group. The covariate is plant size. The treatments are those listed in the text (see also Table 4).

	Covariate		Treatment	
	F	P	F	P
1989 Seed production	37.164	<.001	1.358	.25
1990 Seed production	39.818	<.001	1.854	.12
1989 Growth	27.207	<.001	0.822	.583
1990 Growth	0.893	.346	2.453	.047

Seed production (square root transformed) was a positive linear function of plant size. Overall values of R^2 for regressions of seed production on plant size were .206 in 1989 and .182 in 1990. Slopes of individual regressions for each treatment for seed production on plant size did not differ from the slope for control plants.

Plant size was a minor but important factor influencing both growth and reproduction in A. kentrophyta and indicates that size should be considered as a covariate in an analysis of variance of treatment effects in this experiment. Analyses of covariance (ANCOVA) and experimental results are presented in Tables 3 and 4, respectively. Plant size was a significant covariate in three of four analyses. There were no differences among treatment groups in seed production (reproduction) for either year. Growth did not differ among treatment groups in 1989, but there was a significant difference between groups in 1990 ($P = .047$). A protected least-significant-difference (LSD) test indicates that growth in the Target group was greater than that of individuals in other treatment groups (Table 4).

Table 5 gives the results of two-tailed t tests comparing mean reproduction and growth across years within treatment groups. There were no significant differences for seed production among treatment groups between 1989 and 1990. Average size for plants in 1990 was consistently significantly greater than the size of the same plants the previous year (i.e., on average, plants grew larger over the course of the experiment). The No Predation treatment grew significantly less in 1990 than 1989, whereas plants in the Target group grew significantly more in 1990. There were no significant differences in growth across years for plants in the Control, Fertilized, or Water groups.

A series of simple linear regressions was used to compare seed production with growth to test for the presence of a trade-off between these two primary components of fitness. When the data are corrected for the fact that larger plants are inherently more capable of producing more flowers and fruits, the analysis finds no significant differences among treatment groups (by virtue of overlapping 95% confidence intervals); and, therefore, no trade-off between growth and reproduction within a given year was detected.

To compare trade-offs across years, the ratio of 1990 to 1989 data was used (Table 5). This provides a number >1.0 when 1990 data values exceed 1989 values; the converse is true when results are <1.0. Seed production was greater in 1990 than in 1989 regardless of treatment group. In contrast, growth in 1990 was less than that experienced in 1989 with the notable exception of Target plants. The results can be interpreted as evidence for a trade-off between growth and reproduction. They indicate that, in general, increased seed production is associated with decreased growth. Furthermore, plants may be relieved of trade-off constraints by removing competitors, which should increase availability of mineral resources to the remaining (target) plant.

DISCUSSION

Resource supplementation or alleviation of resource competition did not significantly influence the reproductive output of A. kentrophyta. Instead, seed production was more closely related to the individual's past record of seed output (Tables 1, 3, 5). Plants that produced many seeds in 1989 tended to produce many seeds in 1990, regardless of treatment. Growth, while similarly unresponsive to the addition of single resources, increased significantly when potential competitors were removed (Tables 4,

TABLE 4. Treatment means (SD) in both 1989 and 1990 for important demographic traits.

	Control	No bugs	Fertilized	Water	Target
1989 Seed production	25.8 (25.2	16.1 (11.8)	30.6 (24.5)	25.1 (22.2)	44.2 (41.4)
1990 Seed production	32.2 (32.28)	20.5 (16.7)	39.7 (37.3)	30.7 (27.9)	54.5 (58.4)
1989 Plant size	5997.1 (2851.7)	4594.6 (1871.8)	6833.9 (2892.7)	6333.2 (2891.4)	7683.2 (3683.8)
1990 Plant size	7247.3 (3128.8)	5596.3 (2156.6)	7934.0 (3242.6)	7418.2 (3627.4)	8393.0 (4159.9)
1989 Growth	1478.4 (1329.7)	1530.0 (987.7)	1772.1 (1634.2)	1797.9 (1486.9)	1503.1 (988.6)
1990 Growth*	1156.1 (1529.9)	808.4 (1000.4)	1587.8 (2044.5)	1395.0 (1760.3)	2433.2 (1749.0)

*Growth in 1990 varied significantly among treatments (see Table 3). The Target groups grew more, on average, than did plants in any other treatment group. No other differences were significant.

5). These results differ from those of Wright and Mooney (1965), Mooney (1966), and Marchand (1973), which show that mineral nutrients were the primary factors limiting other species that occur on dolomite in the White Mountains (*Artemisia tridentata*, two *Erigeron* species, and *Lupinus argenteus*, respectively). Korner (1989) reports that the effect of fertilization on the growth of species from nutrient-poor environments is often difficult to detect. He does not cite studies that address the relationship between growth and reproduction in nutrient-supplementation experiments.

The addition of mineral nutrients or water alone may have been insufficient stimuli for *A. kentrophyta* to increase either reproduction or growth if both factors were limiting. Multiple limiting factors have been reported in a variety of species (Harper 1977) and are specifically predicted by Tilman's (1980, 1982) models of optimal resource consumption. That there may be multiple resource limits to *A. kentrophyta* growth and reproduction is supported by the response of *A. kentrophyta* to the removal of competitors in this study.

Tanglefoot barriers were very effective at excluding ground-moving herbivores and predators. This was evidenced by the lack of foliar damage or partially eaten fruit and the capture of many insects in the traps. Flowers of *A. kentrophyta* are produced in sufficient excess to buffer individuals against the levels of flower and fruit predation observed in this population.

Growth in *A. kentrophyta*, as has been reported for a number of species from arid regions throughout the world (Fonteyn and Mahall 1981, Robberecht et al. 1983, Ehleringer 1984, Parker and Salzman 1985, Shaw 1987, Manning and Barbour 1988, and Chapin et al.

1989), is most sensitive to the proximity of its neighbors. It is unclear, however, why reproduction among such species is rarely similarly influenced (as is the case with *A. kentrophyta*). The buffering of fitness components against environmental stochasticity is characteristic of density-vague demographics as described by Strong (1986). Under density-vague conditions, selection favors demographic functions with indeterminate functional thresholds. That is, current allocation decisions are only loosely linked to current environmental conditions (Strong 1986).

Trade-offs between growth and reproduction within years were not observed in this experiment under any conditions. A weak trade-off between growth and reproduction was identified in most treatment groups when data were compared across years (Table 5). It is of great interest that the Target group alone experienced an increase in both seed production and growth in 1990 compared to 1989 values (and thus did not experience a trade-off). The absence of well-defined trade-offs between primary components of fitness could be due to one of several reasons. Lack of a discernible trade-off would be noted if resources were not truly limiting. It may also be that growth and reproduction are not co-limiting for this species in this environment. If this were true, factors that influence growth and reproduction are likely to be independent (e.g., one fitness component might be canalized and the other dependent on environmental conditions). Finally, a trade-off between growth and reproduction would not be detected if a resource other than one provided in this experiment were limiting.

Adult *A. kentrophyta* mortality at the Sheep Mountain study site is low, juvenile mortality is extremely high (even though germination

TABLE 5. Cross-year comparisons of fitness components. 1990 values represented as a fraction of 1989 trait values. Values of t and the associated probabilities (P) represent results of two-tailed t tests for differences in values between years. Refer to Table 4 for raw data.

		Control	No bugs	Fertilized	Water	Target
Seed production	90/89*	1.25	1.16	1.32	1.15	1.18
	t	1.41	1.71	1.80	1.39	0.71
	P	.17	.10	.08	.17	.49
Plant size	t	7.06	5.02	4.90	5.05	3.50
	P	<.01	<.01	<.01	<.01	<.01
Growth	90/89*	0.85	0.98	0.56	0.86	2.07
	t	1.13	2.50	0.40	1.42	2.12
	P	.26	.02	.70	.16	.05

*Values listed represent the ratio of 1990 trait values to those of 1989.

tests under controlled conditions show seed viability of greater than 95%), and recruitment is low (Owen 1991). These demographic attributes would certainly favor a strategy that routes resources away from the risky business of reproduction toward growth. The small but consistent portion of *A. kentrophyta's* annual accumulation of biomass allocated to reproduction guarantees that each plant will probably produce at least a few seeds each year while being able to dedicate most of each season's accumulated resources to growth and survival. That the allocation of resources to reproduction, but not growth, in this species is constant over a broad range of resource availabilities is consistent with a bet-hedging life-history strategy (Kozlowski and Stearns 1989, Philippi and Seger 1989, Stearns 1989).

Resource limitations on organisms are rarely simple or solitary. While fruit and flower predation can be an important limit on fecundity, such an effect was not noted here. Similarly, the reproductive output of plants growing on the Sheep Mountain dolomite barrens would appear to be resource limited, although single resource augmentation had no direct effect on seed production. In combination, however, resources can influence the amount of realized growth that in subsequent years will affect reproduction.

LITERATURE CITED

BARNEBY, R. C. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden 13: 1–1187.

BOOKMAN, S. S. 1983. Costs and benefits of flower abscission and fruit abortion in *Asclepias speciosa*. Ecology 64: 264–273.

BRAYTON, R., AND H. A. MOONEY. 1966. Population variability of *Cercocarpus* in the White Mountains of California as related to habitat. Evolution 20: 383–391.

CHAMBERS, J. C., J. A. MACMAHON, AND R. W. BROWN. 1987. Response of an early seral dominant alpine grass and a late seral dominant alpine forb to N and P availability. Reclamation and Revegetation Research 6: 219–234.

CHAPIN, F. S., J. B. MCGRAW, AND G. R. SHAVER. 1989. Competition causes regular spacing of alder in Alaskan shrub tundra. Oecologia 79: 412–416.

CODY, M. L. 1966. A general theory of clutch size. Evolution 20: 174–184.

EHLERINGER, J. R. 1984. Intraspecific competitive effects on water relations, growth, and reproduction in *Encelia farinosa*. Oecologia 63: 153–158.

FONTEYN, P. J., AND B. E. MAHALL. 1981. An experimental analysis of structure in a desert plant community. Journal of Ecology 69: 883–896.

FOWLER, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17: 443–464.

GRIME, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York, NY.

HALL, C. A., EDITOR. 1991. Natural history of the White-Inyo Range. University of California Press, Berkeley.

HARPER, J. L. 1977. Population biology of plants. Academic Press, New York, NY.

KORNER, C. 1989. The nutritional status of plants from higher altitudes. Oecologia 81: 379–391.

KOZLOWSKI, J., AND S. C. STEARNS. 1989. Hypotheses for the production of excess zygotes: models of bet-hedging and selective abortion. Evolution 43: 1369–1377.

LLOYD, R. M., AND R. S. MITCHELL. 1973. A flora of the White Mountains, California and Nevada. University of California Press, Berkeley.

LOVETT DOUST, J., AND L. LOVETT DOUST. 1988. Plant reproductive ecology. Oxford University Press, New York, NY.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Manning, S. J., and M. G. Barbour. 1988. Root systems, spatial patterns, and competition for soil moisture between desert subshrubs. American Journal of Botany 75: 885–893.

Marchand, D. E. 1973. Edaphic control of plant distribution in the White Mountains, eastern California. Ecology 54: 233–250.

————. 1974. Chemical weathering, soil development, and geochemical fractionation in a part of the White Mountains, Mono and Inyo counties, California. USGS Professional Paper 352-J.

Marquis, R. J. 1991. Evolution of resistance in plants to herbivores. Evolutionary Trends in Plants 5: 23–29.

Mooney, H. A. 1966. Influence of soil type on the distribution of two closely related species of *Erigeron*. Ecology 47: 950–958.

Mooney, H. A., G. St. Andre, and R. D. Wright. 1962. Alpine and subalpine vegetation patterns in the White Mountains of California. American Midland Naturalist 68: 257–273.

Owen, W. R. 1991. The reproductive ecology of an alpine legume: *A. kentrophyta* var. *implexus*. Unpublished dissertation, University of California, Davis. 226 pp.

Pace, N., D. W. Kiepert, and E. M. Nissen. 1968. Climatological data summary for the Crooked Creek Laboratory, 1949–1967, and the Barcroft Laboratory, 1953–1967. University of California, White Mountain Research Station Publication, Berkeley.

Parker, M. A., and A. G. Salzman. 1985. Herbivore exclosure and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. Journal of Ecology 73: 903–913.

Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology and Evolution 4: 41–44.

Robberecht, R., B. E. Mahall, and P. S. Nobel. 1983. Experimental removal of intraspecific competitors— effects on water relations and productivity of a desert bunchgrass *Hilaria rigida*. Oecologia 60: 21–24.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122: 240–285.

Shaver, G. R., and F. S. Chapin. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61: 662–675.

Shaw, R. G. 1987. Density dependence in *Salvia lyrata*: experimental alterations of densities of established plants. Journal of Ecology 75: 1049–1063.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W.H. Freeman and Company, New York, NY.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3: 259–268.

Stephenson, A. G. 1984. The cost of over-initiating fruit. American Midland Naturalist 112: 379–386.

Strong, D. R. 1986. Density vagueness: abiding the variance in the demography of real populations. Pages 257–268 *in* J. Diamond and T. J. Case, editors, Community ecology. Harper and Row Publishers, New York, NY.

Tilman, D. 1980. Resources, a graphical-mechanistic approach to competition and predation. American Naturalist 116: 362–393.

————. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

Weiner, J. 1988. Variation in the performance of individuals in plant populations. Pages 59–81 *in* A. J. Davey, M. J. Hutchings, and A. R. Watkinson, editors, Plant population ecology. Blackwell Scientific Publications, London.

————. 1990. Resource competition and community structure. Trends in Evolution and Ecology 5: 360–364.

Welden, C. W., and W. L. Slausen. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61: 23–44.

Wright, R. D., and H. A. Mooney. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. American Midland Naturalist 73: 257–284.